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Résumé

La *Thamnophis sirtalis parietalis*, une sous-espèce de la couleuvre rayée, atteint la limite septentrionale de son aire de distribution dans la région située entre les lacs Winnipeg, Winnipegosis et Manitoba. En dépit du climat rigoureux et instable qui sévit dans cette région, l'espèce y prolifère. Cette étude vise à expliquer, en termes d'écologie, les raisons de cette abondance.

Les populations de *Thamnophis sirtalis* habitant cette région du Manitoba sont importantes, mais elles sont soumises à des fluctuations considérables. La principale cause de la baisse de population est due à une incapacité de l'espèce à se reproduire dans des conditions climatiques peu favorables, plutôt qu'à l'inégalité des chances de survie des adultes. Bien que la période de croissance soit brève, les femelles peuvent probablement atteindre leur maturité sexuelle à trois ans et parfois, à deux ans. Le potentiel reproductif est apparemment plus élevé que chez certaines des populations méridionales, mais le nombre de couleuvreaux par portée est à peu près le même. Les autres aspects du cycle reproductif des mâles et des femelles ressemblent fondamentalement à ceux de leurs congénères vivant ailleurs. On estime que, sur toute son aire de distribution, la *T. sirtalis* se rapproche par ses traits fondamentaux d'une espèce sélectionnée pour sa capacité de reproduction (sélection-r). Toutefois, le cycle annuel des populations de la région étudiée présente des caractéristiques inhabituelles; leur sortie au printemps, par exemple, et leur comportement nuptial sont fort complexes, et leur dispersion estivale s'effectue dans un très vaste rayon. Tous ces facteurs ont une influence considérable sur leur survie.

Summary

The red-sided garter snake, *Thamnophis sirtalis parietalis*, approaches the northern limit of its range in the Interlake of Manitoba, Canada. Although the climate is extreme and variable, the species is abundant in this region. The overall objective of this study was to explain this abundance in ecological terms.

Denning populations of *T. sirtalis* in the Interlake are large, but they are susceptible to great fluctuation in size. The main cause of population declines may be reproductive failure, resulting from poor weather conditions, rather than variable survivorship of adults. Despite the short growing season, juvenile female snakes probably grow rapidly enough to reproduce for the first time by at least the third year of life, and sometimes by the second. The number of young per litter is approximately the same as in more southerly populations, although Interlake females seem to have the potential to produce larger litters than observed in this study. Other aspects of the reproductive cycles of both males and females are basically similar to those known for the species elsewhere. It is suggested that *T. sirtalis* resembles an "r-selected" species throughout its range. The annual cycle of the Interlake populations, however, includes unusual features, such as complex spring emergence and mating behaviour and long-distance summer dispersal, which may be important aspects of life-history strategy in this environment.

Biographical Note

Patrick T. Gregory was born in Bilston, England, in 1946 but he has spent most of his life in Canada. He received his B.Sc. in 1969 from the University of Toronto and then went to the University of Manitoba, where he received his M.Sc. in 1971 and Ph.D. in 1974. Currently, he is assistant professor in the department of biology at the University of Victoria, Victoria, B.C., where he has been working since 1973. His major research interests are the population dynamics and general ecology of amphibians and reptiles, most particularly snakes. He has published several papers and notes on snake ecology. Dr. Gregory is a member of the American Society of Ichthyologists and Herpetologists, the American Society of Naturalists, and the Ecological Society of America.

Acknowledgements

I wish to express my appreciation to the following members of the faculty at the University of Manitoba: Dr. K.W. Stewart, for his supervision and advice during all stages of this study and the preparation of the thesis from which this paper is derived; Dr. R.H. Green, who offered much advice on statistical techniques and, with Drs. M. Samoiloff and J.R. MacKay, gave a critical evaluation of the thesis; and Dr. A.N. Arnason, who provided me with much valuable information concerning the use of mark–recapture methods. Ms. Catherine M. Carr and Mr. Hugh Barclay (University of Victoria) commented on later versions of the manuscript. Thanks are also due to Messrs. W.J. McKague and W.J.S. McKague of Inwood, Manitoba, who allowed me access to a large hibernaculum on their property. I was ably assisted in my field-work by Mr. Don Hart, and our friends Jason and Gandalf. Special thanks are due to Dr. H.S. Fitch of the University of Kansas, for acting as the external examiner of the thesis version of the paper. His comments were invaluable.

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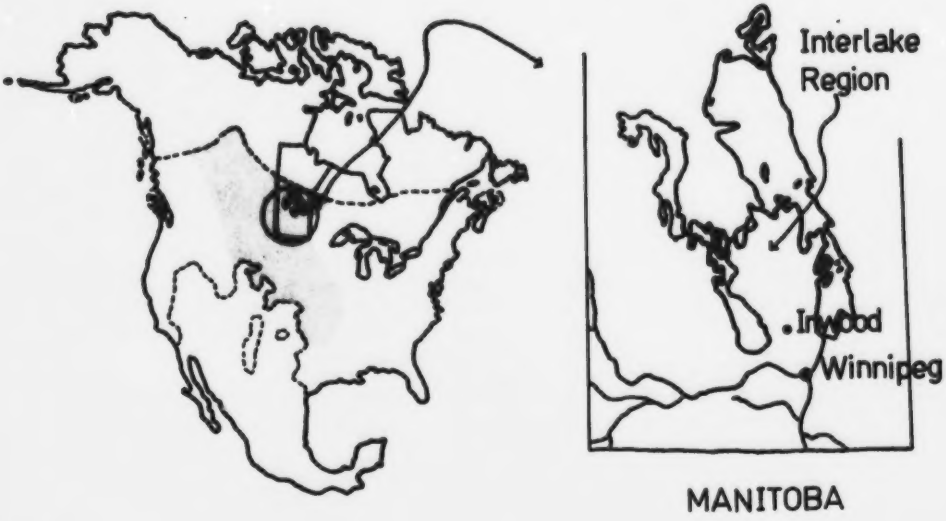

Figure 1
Map of North America showing distribution of *Thamnophis sirtalis*; inset shows study area in Manitoba. Broken line indicates range of *T. sirtalis*, and shaded area shows range of subspecies *parietalis* (after Fitch 1965:504).

Introduction

The red-sided garter snake, *Thamnophis sirtalis parietalis*, approaches the northern limit of its distribution in the Interlake region of Manitoba (Figure 1). The short and variable growing season in this area is apparently reflected in the annual cycle of these snakes. They spend six or more months of the year in hibernation, and are completely absent from hibernacula for only about three months of every year (Gregory 1971, 1974; Gregory and Stewart 1975). Large fluctuations in population size seem to occur.

Despite this, *T. sirtalis* appears to be a very abundant species in the Interlake. Young snakes are rarely seen, but the adults are particularly evident in spring and fall because of their habit of overwintering in large communal aggregations, sometimes numbering in the thousands (Gregory 1971). This impression of abundance is further reinforced by their mass migrations to marshes in spring and back to hibernacula in autumn (Gregory 1971; Gregory and Stewart 1975). Such large overwintering populations and large-scale movements are not known for the species at lower latitudes.

These observations suggested that the Interlake red-sided garter snake populations might provide a model for the study of ecological adaptation to a northern and nearly limiting environment. The relative wealth of literature (Carpenter 1952*b*; Fitch 1965) concerning the ecology of the species farther south provided a suitable basis for comparison. Also, the presence of large, apparently distinct populations at discrete denning areas (Gregory 1971) afforded a unique opportunity to investigate in detail the long-term population dynamics of this species. The following questions were of particular interest in this study:

(a) Do population sizes fluctuate as greatly as appears to be the case? Do any changes in survivorship, fecundity, and sex or age composition accompany such fluctuations, and what might they caused by?

(b) Are growth, fecundity, and age of first reproduction comparable with those of more southerly populations, where the growing season is longer (Carpenter 1952*a*; Platt, personal communication)? Are there any major differences in life-history strategies of northern and southern populations?

(c) Do individual females reproduce every year or do they follow a cycle of two or more years, as is the case for many species of snakes inhabiting high altitude or latitude localities (Rahn 1942; Saint Girons 1957; Prestt 1971)?

Figure 2
Photograph of Den One.

Materials and Methods

The Study Area

This study was carried out in the Interlake region of Manitoba, in the vicinity of the town of Inwood, about 71 km northwest of Winnipeg (Figure 1). This is the same study site described in Gregory (1971) and Gregory and Stewart (1975).

The area consists of a system of alternating linear ridges and depressions oriented in a northwest–southeast direction. For the most part, the depressions consist of marshes, with small lakes or ponds in the middle of the larger marshes. These marshes are inhabited by *T. sirtalis* during the summer (Gregory and Stewart 1975). The ridges are forested and consist of fissured limestone outcrop, which often slumps into subterranean caves, forming "sinks" and providing access underground. *T. sirtalis* uses these sinks as dens or hibernacula.

Inwood is situated on one of the more southerly ridges. The area immediately around the town is dotted with hibernacula, several of which have apparently been used for many years. The locations of known dens are shown in Gregory and Stewart (1975). An example of a hibernaculum, and the one that has been studied most intensively, is Den One (Figure 2). This den is a large oval-shaped limestone sink about 20 m long by 12 m wide and 3 m deep, and is located approximately 1.5 km southwest of Inwood. The bottom of this bowl-like depression is well-fissured and littered with pieces of rock.

The extreme climate at this latitude in Manitoba is indicated by meteorological records for the city of Winnipeg, which has slightly milder weather (Weir 1960) than the study area. From 1969 to 1972 inclusive, the longest period free of killing frost (that is, air temperature $\leq -1.4°C$) was 137 days; in 1969 this period was only 95 days. The longest frost-free period in those four years was 109 days. Also, the variation in air temperature within a given day, and among different days, is very great, even during the summer (Figure 3). The percentage of possible sunshine is high during the summer, and annual precipitation is generally low (Figure 3).

Methods

Every spring and fall, from autumn 1969 to spring 1973 inclusive, samples of snakes were taken by hand from Den One on an almost daily basis. Snakes are active in the vicinity of dens for as long as one and one-half to two months in these seasons (Gregory 1971). Each previously uncaught snake was sexed, measured (snout to vent length, hereafter abbreviated as S–V length) to the nearest 5 mm, and individually marked by removing subcaudal scutes, after the method of Blanchard and Finster (1933), using the code described in Gregory (1971). All recaptured animals were noted and measured. Similar data were occasionally collected from other dens. Analysis of the population structure of Den One was based on the size-frequency distributions obtained for each sex; average lengths were used for individuals that were measured more than once in a given season. Separation into age–size groups was attempted by using Cassie's (1954) probability paper technique.

Two mark–recapture methods were used to estimate the size of the Den One population each year. In estimating population sizes, the sexes were treated separately, so that sample heterogeneity was minimized. Petersen indexes (Robson and Regier 1968) of the number of snakes entering the den every fall were calculated by considering each autumn a marking period, and the subsequent spring a recapturing period. This method was applicable because there was no recruitment between sampling times. The Petersen index was used for both sexes.

Jolly's (1965) unrestricted multiple-sample model, which allows both death and recruitment, was also used, since the number of sampling periods (eight) and the sample sizes obtainable appeared sufficiently large for meaningful estimates to be expected, at least for the males. In addition to estimating both spring and autumn population sizes, the Jolly model also estimates probabilities of survivorship between sampling periods and their variances. Recruitment estimates were not calculated, since variances of B_i in the unrestricted Jolly model tend to be very large (Carothers 1973), rendering the estimates meaningless. The possibility of unequal catchability (due to some animals moving from den to den in different years) was assessed by calculating the percentage of previously captured snakes that returned to the same dens one summer or more after original marking. Unequal catchability of marked animals at Den One was also tested using Leslie's (1958) method.

Increases in S–V lengths of marked snakes found at dens in two successive overwintering periods were used to estimate annual

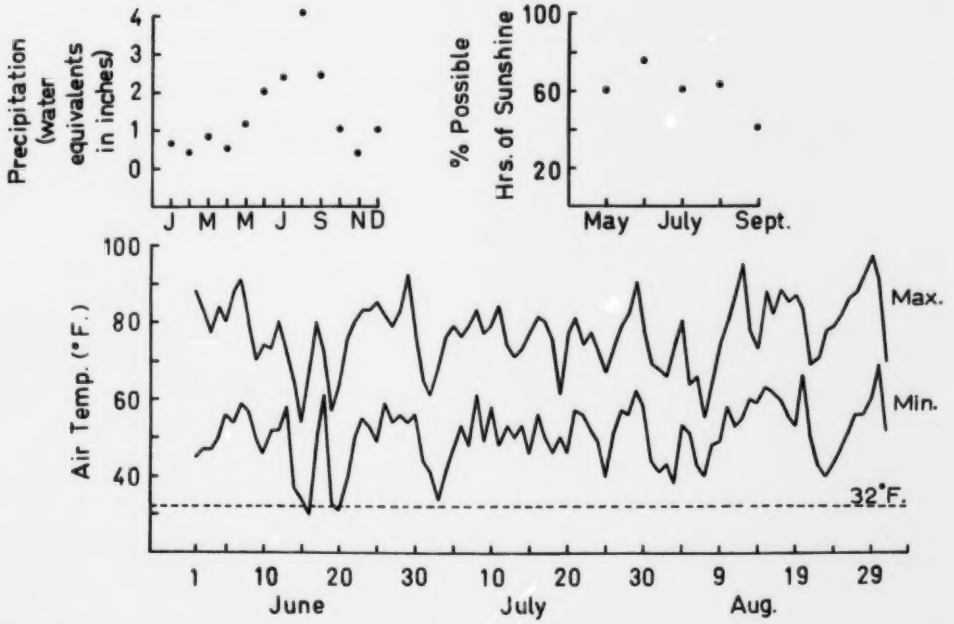

Figure 3
Winnipeg weather records for 1972.

growth. The Walford (1946) analysis was employed because all snakes at the dens under observation appeared to be in at least their second year of life and were presumably past the period of rapid growth that marks early life (Gregory 1971). Growth rates among years were compared by analysis of covariance.

Potential fecundity in denning populations was estimated from samples of female snakes from the vicinity of Inwood. Estimates for 1972 were based on snakes collected in late April and May from roads within 3 km of Inwood and from dens throughout the spring. Reproductive potential for 1973 was assessed from samples of females from dens in autumn 1972 and spring 1973. No snakes were taken from Den One. The lengths of all ovarian ova were measured to the nearest 0.1 mm, and the data were broken into size groups by probability paper analysis (Cassie 1954). It was assumed that the group of largest eggs represented the mature ova (Cieslak 1945; Bragdon 1952; Tinkle 1962; Betz 1963*b*). This was checked by comparing the sizes of the remaining ova with those of immature eggs left in the ovaries of females that had ovulated later in the spring. Reproductive potentials in the two years were compared by analysis of covariance.

Females were collected throughout 1972 and their reproductive tracts were examined. Realized fecundity (fertility) was measured by counting the number of apparently viable young *in utero* in females that were in advanced stages of gestation. Potential litter sizes (that is, the number of mature eggs ovulated) were also estimated for these females by counting the ovulation scars in their ovaries. Additional information on litter sizes was obtained from gravid females that were kept in an outdoor enclosure at the University of Manitoba in the summer of 1972 and that were allowed to give birth in the laboratory before being killed. The young snakes were measured (S–V length to nearest millimetre) and sexed by dissection.

All dissected females were checked for copulatory plugs in their cloacae and for sperm in their oviducts as indicators of recent mating. Times of ovulation, stages of embryonic development (Zehr 1962), and times of birth were also estimated from dissections. Reproductive tracts of obviously postpartum females (as indicated by uterine and ovulation scars) were qualitatively examined to determine if these snakes would be able to breed again the next year.

Males were also collected throughout 1972. These were checked for the presence of sperm in each testis, epididymis, and vas deferens by crushing each organ on a microscope slide and examining the slide under a binocular microscope. No attempt was made to estimate abundance of sperm in each sample. A plot was made of total weight of testes per millimetres S–V length vs. time, for the entire period, after the method of Fox (1952, 1954).

The rejection level used in all statistical tests was the conventional $\alpha = 0.05$.

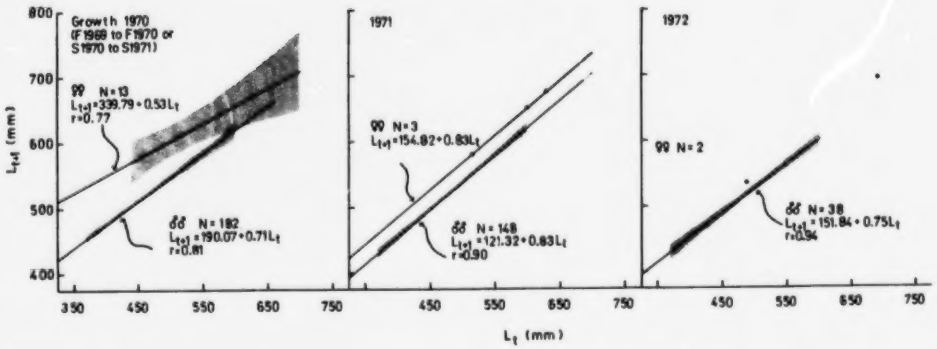

Figure 4
Walford plots of growth of both sexes for 1970, 1971, and 1972. Dots indicate measurements of females; shaded areas are 95% confidence bands about means of regressions. F = fall; S = spring; N = sample size.

Results

Growth

In the case of male snakes, the time intervals used in the growth analysis were fall-to-fall and spring-to-spring, the former being chosen when both were available for a given snake in a particular year. This was done to minimize variability caused by the growth spurt that seemed to take place in spring shortly after emergence from hibernation. This growth was detected through the repeated capture of individual snakes at Den One in spring; the increase in S–V length was sometimes as much as 20 mm and appeared to be the only part of the annual growth occurring at the den sites. In the case of females, for which many fewer data were obtained, S–V length measurements taken at any time in two successive denning periods were used, unless the preferred intervals were available. In all instances the figures used were averages of all the times the particular animal was measured in a given spring or fall.

A total of 368 growth measurements were obtained for males: 182 for 1970, 148 for 1971, and 38 for 1972. Only 18 were obtained for females: 13, 3, and 2 for 1970, 1971, and 1972 respectively. Several individuals were included in more than one year through repeated annual recaptures. The data were plotted in the form L_{t+1} vs. L_t (L = S–V length in millimetres; t = overwintering period), and the linear regressions of L_{t+1} on L_t were calculated along with the 95% confidence limits about their means (Figure 4). The confidence bands are missing for females in 1971 and 1972 since, in the first case, the nearly perfect linear relationship of the three points resulted in misleadingly narrow confidence limits and, in the second case, only two points were available.

The analysis of covariance was applied separately to the regressions for each sex. The 1972 data for the females were not used in this analysis. In the case of the males, the assumption of homogeneity of within-group variances was not satisfied, Bartlett's chi-square (Snedecor and Cochran 1967: 296–98) being barely significant ($p < 0.05$). The differences among the adjusted means of the three groups were, however, highly significant ($p < 0.01$), suggesting that the lines were probably different. Bartlett's chi-square also indicated significant heterogeneity of within-group variances ($p < 0.01$) for the females, invalidating the analysis.

Population Characteristics

Population Dynamics

Tests of Assumptions

Not all of the assumptions of mark–recapture methods are testable, but most can be assessed, at least indirectly. Since the den area is small, it can be assumed that dispersal of marked animals was complete between sample times. Recently marked animals were captured at all parts of the den. The probability of survival was probably fairly constant within each sex at any one time, since the population was apparently all adult (Gregory 1971), and differences in survival rates in animal populations are usually more pronounced between adults and young than among mature age-groups. The mark itself should not have affected the survival rate, since it was inconspicuous and did not appear to impair the snakes in any way (Gregory 1971).

In the Jolly analysis, all animals that leave the population must do so permanently; animals that leave the population temporarily are uncatchable during their absence, and therefore bias the estimates. In this study, 610 instances were recorded of male snakes returning to dens in the Inwood area in denning periods after the one in which they were originally marked. Of these, 586 (96.1%) represented returns to the den of origin. In the case of females, the equivalent figures were 30 and 29 (96.7%). No animals were recorded moving from one den to another and then moving back again. A complete test of the validity of the assumption of equal catchability cannot be made. Leslie's (1958) test, however, was used to test for equal catchability of marked animals. It was not possible to reject the null hypothesis of equal catchability. Leslie's test could not be performed on the female data because there were so few.

Population Size and Survivorship Estimates

The results of the Jolly and Petersen estimates are shown in Table 1. It was not possible to apply the Jolly model to the female data because of the small samples obtained, which was partly a result of the low probability of capture of females in spring (Gregory 1971, 1974).

The Den One population apparently dropped from a high level in 1969–70 to about half that size for the next two winters. The estimates for 1972–73 are of little value because of their very large standard errors. Survivorship of the

Table 1
Population-size changes and survivorship in overwintering populations at Den One, fall 1969 to fall 1972

	Sample period	Number caught & marked	Number of n_i released	Recapture categories				Population size (Jolly)		Population size (Petersen)		Survivorship to next sampling period	
	i	n_i	s_i	$n_{i+1,i}$	m_i	R_i	Z_i	$\hat{N}_i$	S.E.($\hat{N}_i$)	$\hat{N}_i^P$	S.E.($\hat{N}_i^P$)	$\hat{\phi}_i$	S.E.($\hat{\phi}_i$)
Males	Fall 1969	640	638	100		168				5544.22	476.80	0.615	0.059
	Spring 1970	869	868		100	202	68	3407.45	420.00			0.616	0.092
	Fall 1970	90	90	29	25	32	245	2570.42	570.81	2762.07	415.14	0.588	0.092
	Spring 1971	890	890		238	158	39	1711.61	153.78			0.470	0.056
	Fall 1971	221	221	66	56	67	141	2056.39	321.85	2832.82	280.17	0.512	0.091
	Spring 1972	846	845		199	50	9	1492.77	238.56			0.702	0.259
	Fall 1972	130	130	8	17	8	42	5347.86	2285.49	5248.75	1775.13		
	Spring 1973	323	323		50								
Females	Fall 1969	341	339	7						2712.00	948.66		
	Spring 1970	56	56										
	Fall 1970	80	78	4						1462.50	693.08		
	Spring 1971	75	72										
	Fall 1971	198	198	8						1732.50	564.80		
	Spring 1972	70	70										
	Fall 1972	122	122	3						976.00	520.83		
	Spring 1973	24	24										

$$\hat{N}_i = \frac{n_i}{m_i}\hat{M}_i \quad \text{where} \quad \hat{M}_i = \frac{s_i Z_i}{R_i} + m_i$$

$$\hat{N}_i^P = \frac{s_i n_{i+1}}{n_{i+1,i}}$$

$$\hat{\phi}_i = \hat{M}_{i+1}/\hat{M}_i - m_i + s_i$$

All notations as in Jolly (1965), except for the symbol $\hat{N}_i^P$ (Petersen estimate).
Formulae for estimated variances of $\hat{N}_i$ and $\hat{\phi}_i$ in Jolly (1965), for $\hat{N}_i^P$ in Robson and Regier (1968).

males was fairly similar in all years and for the summer and winter periods within each year. Again, the final estimate is a poor one.

Figure 5 shows the changes in the male population. The 95% confidence limits shown are asymmetrical because they were calculated on the basis of the estimated standard error (S.E.) of $1/\hat{N}$, which is more normally distributed than $\hat{N}$ (Ricker 1958). Seber (1973: 7–9) outlines a method whereby the estimated S.E. of $1/\hat{N}_i$ can be calculated; using that method, S.E. $(1/\hat{N}_i)$ is $\sqrt{\hat{V}(\hat{N}_i)/(\hat{N}_i)^4}$. This formula was used for all Jolly estimates. In the case of the Petersen estimates, S.E. $(1/\hat{N}_i)$ was taken to be $\sqrt{n_{i+1,i}(n_{i+1} - n_{i+1,i})/s_i^2 n_{i+1}^3}$ (Ricker 1958). The notation used is that of Jolly (1965).

Population Structure

Figures 6 and 7 show the size-frequency distributions of animals measured at Den One during the eight sampling periods of this study. In each case, the animals used were only those measured in samples taken to estimate population size, and they were grouped into intervals of 10 mm S–V length.

Overlap of size classes was great, particularly in the highly variable females. Attempted separation using Cassie's (1954) method was unsatisfactory. Only the size class of the smallest animals could be differentiated in each case, and only in the males was it very clear. In this group the mean size of the males was about 440–450 mm S–V length and that of the females about 520–530 mm. This size category constituted the dominant group in each instance, except for the fall of 1970 and the spring of 1971.

Sex composition of the denning populations was analysed using the autumn samples. Spring samples could not be used because the catchability of females was low in spring and they were underrepresented in these samples (Gregory 1971, 1974). In autumn, however, there were no obvious behavioural differences between the two sexes, and there was no reason to believe that autumn samples did not constitute simple random samples from the whole population. On this basis, the proportions of males in autumn samples were 0.652 (S.E. = 0.015), 0.529 (S.E. = 0.038), 0.527 (S.E. = 0.024), and 0.516 (S.E. = 0.032) for 1969, 1970, 1971, and 1972 respectively. Standard errors were estimated using the formula S.E. = $\sqrt{PQ/n-1}$, where P = proportion of males in sample, Q = proportion of females, and n = sample size (Cochran 1963: 51). These calculations were based on total numbers of individuals caught in each season, and not on total numbers of captures.

Reproduction

Females

Potential Fecundity

Potential fecundity for 1972 was estimated from dissections of 64 female snakes; estimates of reproductive potential for 1973 were based on 40 specimens from the fall of 1972 and 20 from the spring of 1973.

In both years, smaller females tended to be non-reproductive (Table 2). Potentially reproductive females were generally those which contained ova that were longer than 3 to 4 mm. Agreement was good between separations of egg-size groups based on frequency analysis and those based on dissections of females that had ovulated later in 1972. Very large females tended to have larger ova in both immature and mature categories than did smaller snakes.

Of the 94 potentially reproductive females collected, 89 were examined completely: 53 from spring 1972, 26 from fall 1972, and 10 from spring 1973. The autumn 1972 and spring 1973 samples were combined to estimate reproductive potential for 1973. Potential brood size was plotted against S–V length of female for both years, and a linear relationship was evident in both cases. The assumptions of the analysis of covariance were completely satisfied, so that the two regressions could be compared; the difference between the adjusted means of the two groups was significant ($p < 0.05$). The two lines with the 95% confidence bands about their means are shown in Figure 8.

Of the 64 female snakes in the 1972 spring sample, 24 were obtained from roads. Presumably, these females were dispersing from dens for the summer. Of the 24, 16 showed evidence of recent mating in the form of live sperm in one or both oviducts. All 16 were judged to be potentially reproductive on the basis of an examination of their ovaries. Of the other 8, none of which showed any evidence of recent mating, 4 contained apparently mature ova. In addition, 7 more females, all captured in the presumed summer habitat, were dissected during the month of May in 1972. Four of these were sexually mature and had mated, but the others were not yet able to

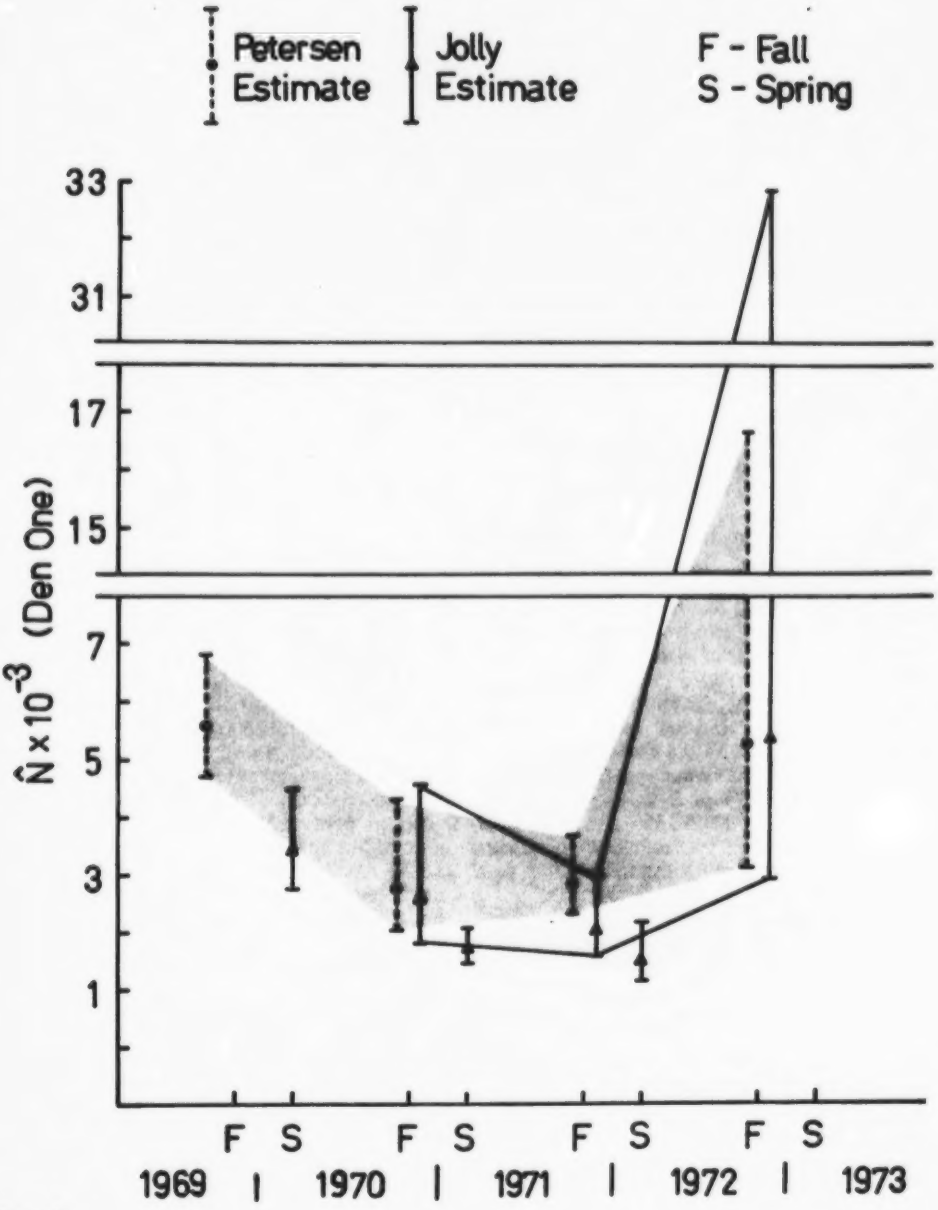

Figure 5
Changes in numbers ($\hat{N}$) of male snakes at Den One from fall 1969 to fall 1972. Marked-off areas represent population changes on a fall-to-fall basis. Vertical lines are 95% confidence limits about estimates.

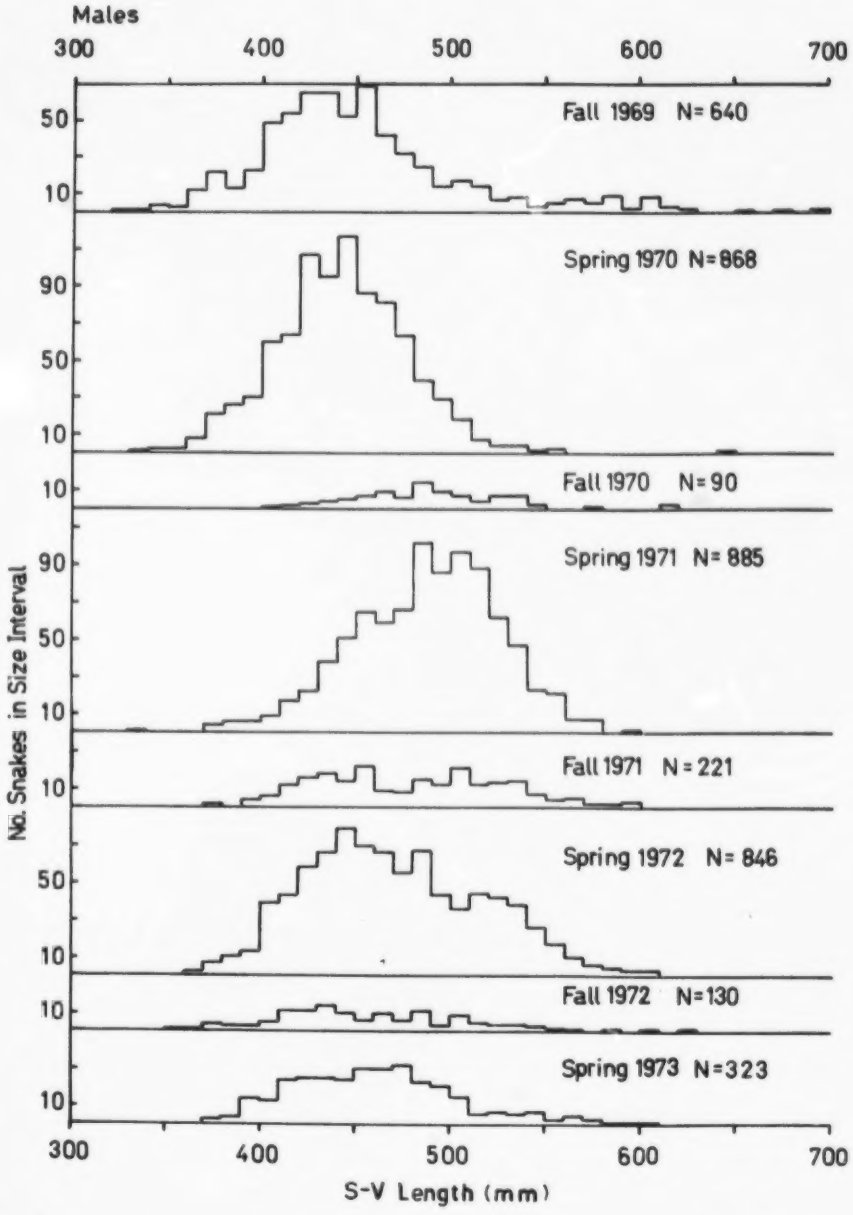

Figure 6
Size-frequency distributions of male snakes at Den One from fall 1969 to spring 1973. Animals are grouped into intervals of 10 mm S–V length. N = sample size.

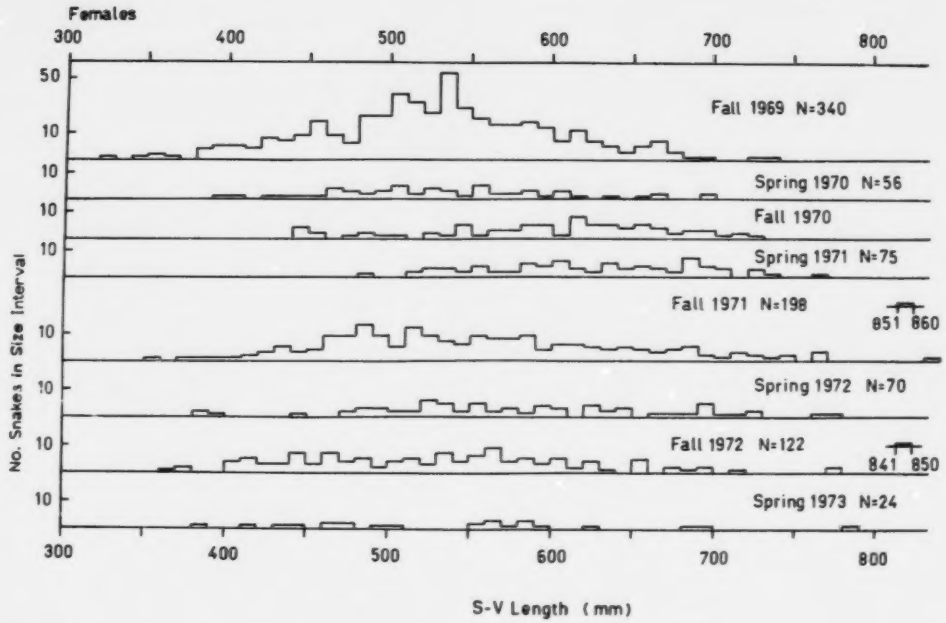

Figure 7
Size-frequency distributions of female snakes at Den One from fall 1969 to spring 1973. Animals are grouped into intervals of 10 mm S–V length. N = sample size.

Table 2
Percentages of reproductive females in different size groups for overwintering seasons of 1971–72 and 1972–73

S–V	Spring 1972			Fall 1972			Spring 1973			Total		
Length (mm)	R*	NR*	%R	R	NR	%R	R	NR	%R	R	NR	%R
–400		1	0.0					2	0.0		3	0.0
401–450	1	2	33.3		3	0.0	3	5	0.0	1	10	9.1
451–500	9	5	64.3	3	4	42.9	1	2	33.3	13	11	54.2
501–550	19		100.0	8	2	80.0	5	1	83.3	32	3	91.4
551–600	11		100.0	6	2	75.0	3		100.0	20	2	90.9
601–650	9		100.0	7	1	87.5				16	1	94.1
651–700	5		100.0	3		100.0	1		100.0	9		100.0
701–	2		100.0	1		100.0				3		100.0

*R = potentially reproductive
*NR = non-reproductive

reproduce and apparently had not mated. The distributions of sizes of all the animals in the mated and non-mated categories are shown in Figure 9.

Development of Young and Realized Fecundity

In 1972, ovulation was first observed as having occurred in a female collected at a den on May 17 and dissected on May 24. Its occurrence was next noted in a female on June 1, and was commonly noted from June 16 on. Ovulated eggs were yolky, somewhat spherical in shape, and much larger than the normal ovarian eggs, which were white and elliptical. One snake dissected on 30 June 1972 had mature ovarian eggs containing yolk but had not yet ovulated. The appearance of eggs in oviducts was concurrent with the appearance of fleshy yellow ovulation scars in the ovaries.

The early stages of embryonic development were not distinguished in this study, and females bearing embryos at these stages were simply noted as having ovulated. Females with embryos well enough advanced for their stages of development to be readily identified began appearing on June 17. All gravid females were caught in summer areas. The earliest births were on about July 28, when five broods were produced by females in transit from the field to the laboratory. Births continued well into September, but all of these were from females that had been kept in laboratory conditions since the end of July. Postpartum females began appearing in the summer areas on August 9.

Figure 10 shows the embryonic development of these animals, based on dissections of 47 females. The stages shown are those of Zehr (1962), and the dates indicate when the animals were dissected, except in instances when the snakes were killed and frozen shortly after capture. Whenever exact dates were not known, the midpoint of the time interval over which the event must have occurred was used. Postpartum females are shown in this figure only if they were captured away from the denning area.

Realized fecundity was lower than potential fecundity, particularly in smaller females. Most gravid females had fewer eggs in their oviducts than ovulation scars in their ovaries, and it was apparent that eggs from the right ovary often entered the left oviduct and vice versa. In many cases, eggs seemed to fail to develop at all *in utero*, or small, malformed embryos accompanied normal-looking ones.

The number of apparently normal young borne by a female was linearly related to the number of ovulation scars in the ovaries of that female (Figure 11). These data are from 16 snakes dissected in various stages of gestation in 1972. Snakes that had just given birth were not used, since there appeared to be some disintegration of ovulation scars by this time, and I did not feel that a reliable count of them could be made.

Twenty-two female snakes used in this study gave birth in 1972. Five broods were born together, however, and some young escaped from three other broods. In most cases, a number of apparently normal young

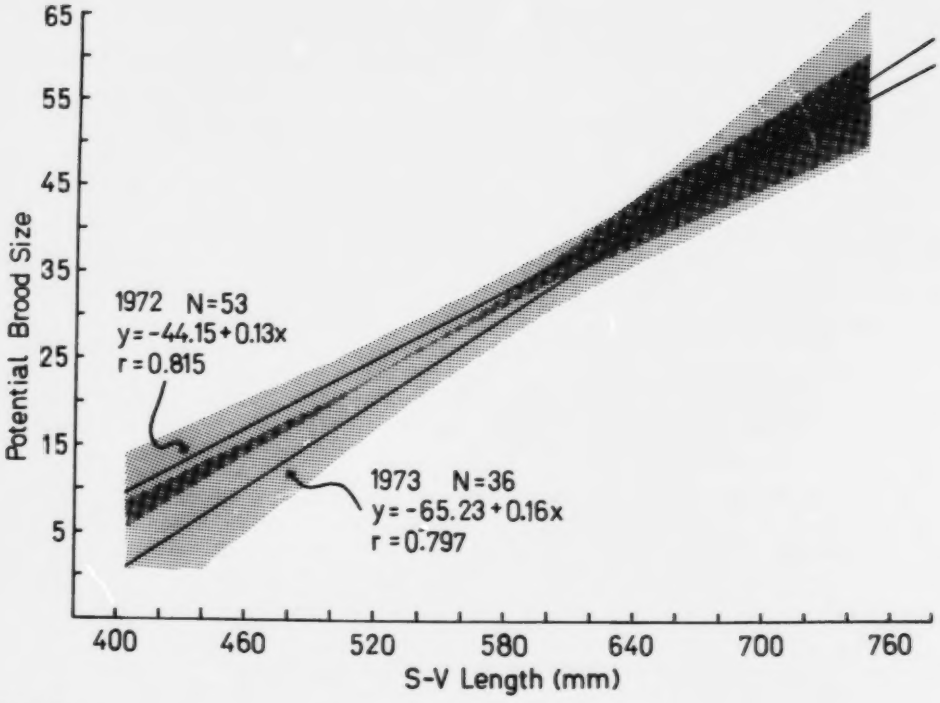

Figure 8
Regressions of potential brood size on size of females overwintering just prior to the 1972 and 1973 breeding seasons. Shaded areas represent 95% confidence bands about means of regressions. N = sample size.

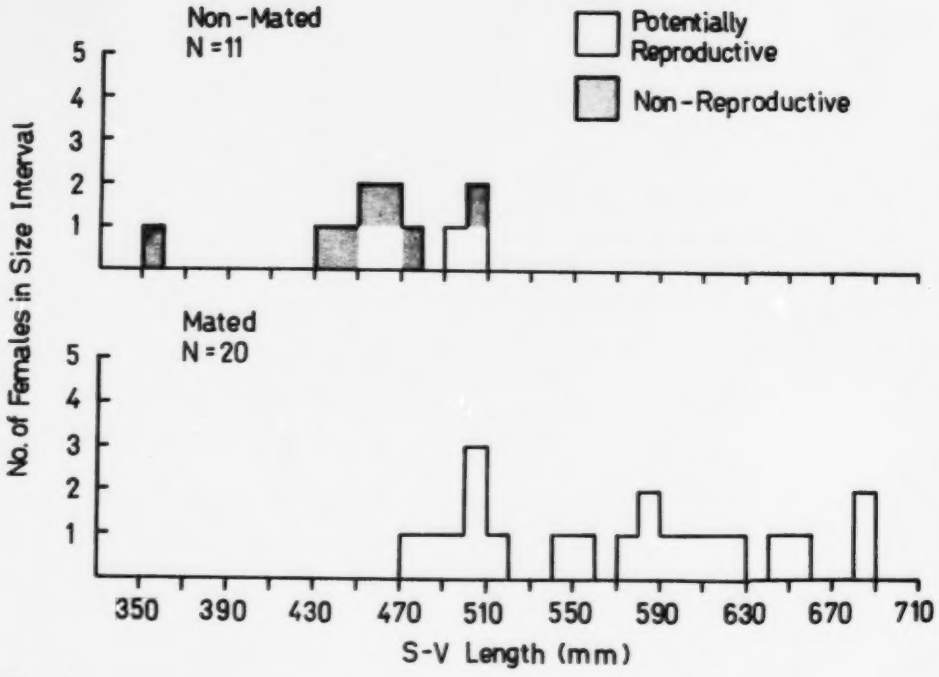

Figure 9
Distribution of potentially reproductive and non-reproductive individuals in mated and non-mated categories of dispersing females in spring 1972. Animals are grouped into intervals of 10 mm S–V length. N = sample size.

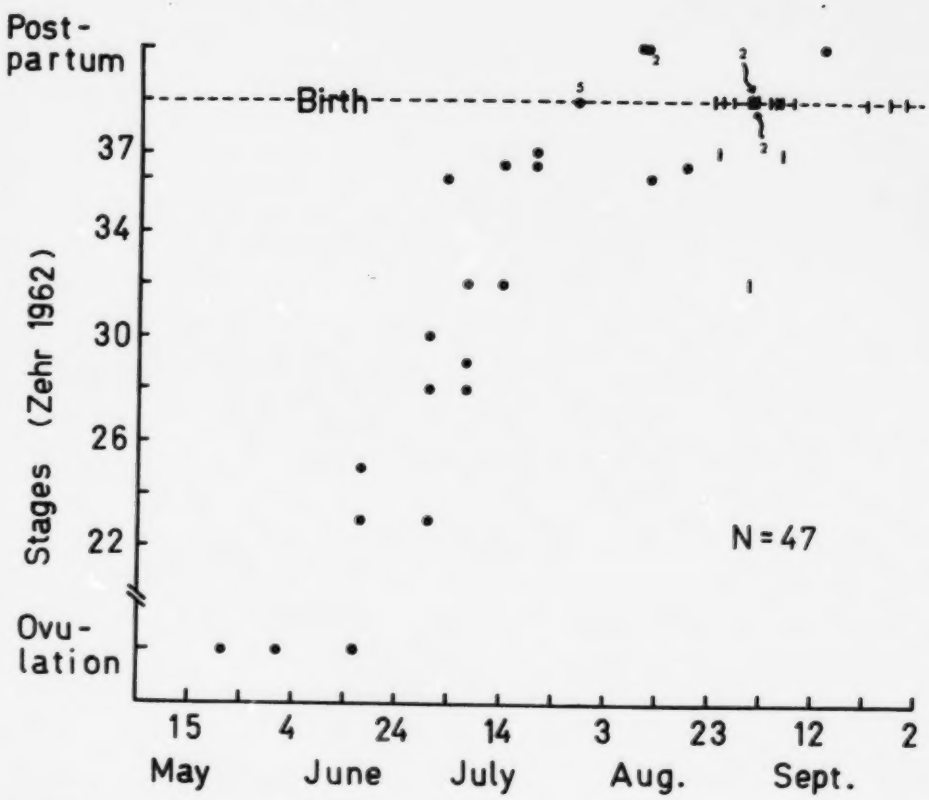

Figure 10
Embryonic development and times of parturition in female snakes from summer 1972. Numbers indicate sample sizes greater than one. Dots = snakes caught in summer areas; vertical lines = captive specimens; N = sample size.

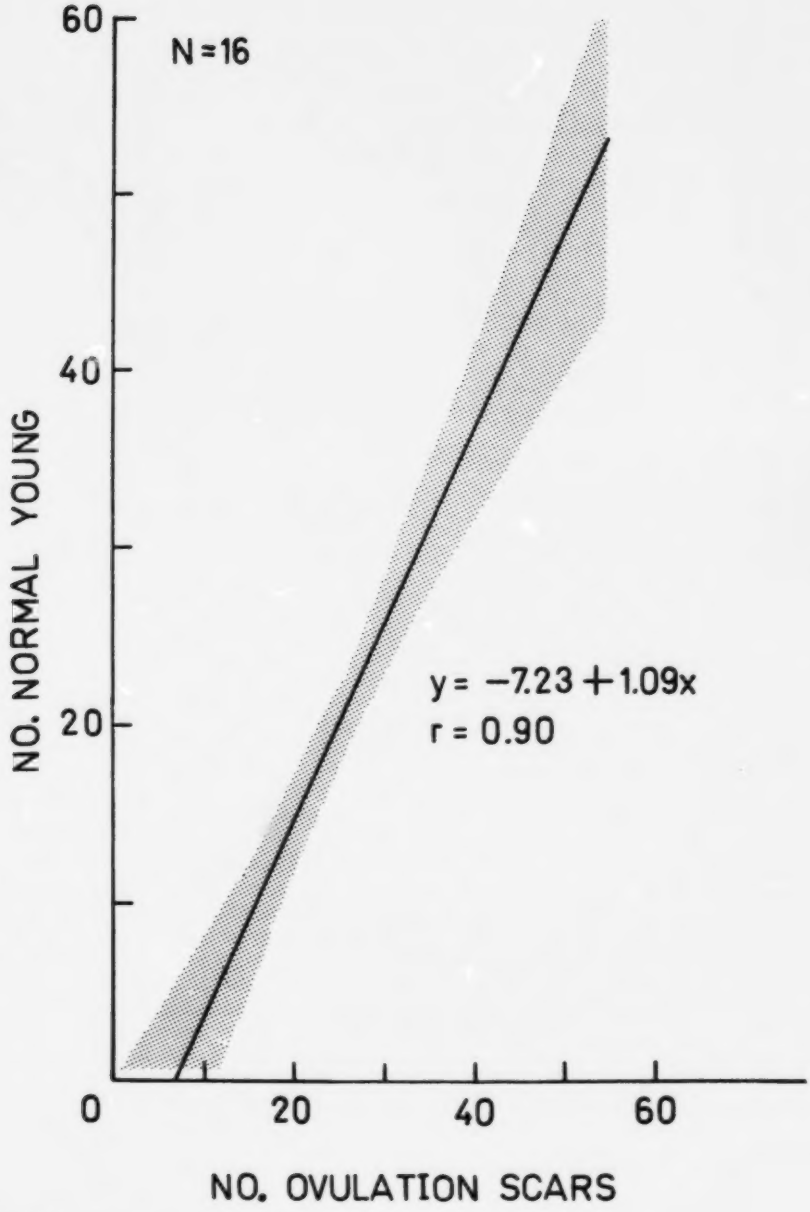

Figure 11
Regression of number of normal young on number of ovulation scars for females from summer 1972. Shaded area represents 95% confidence band about mean of regression. N = sample size.

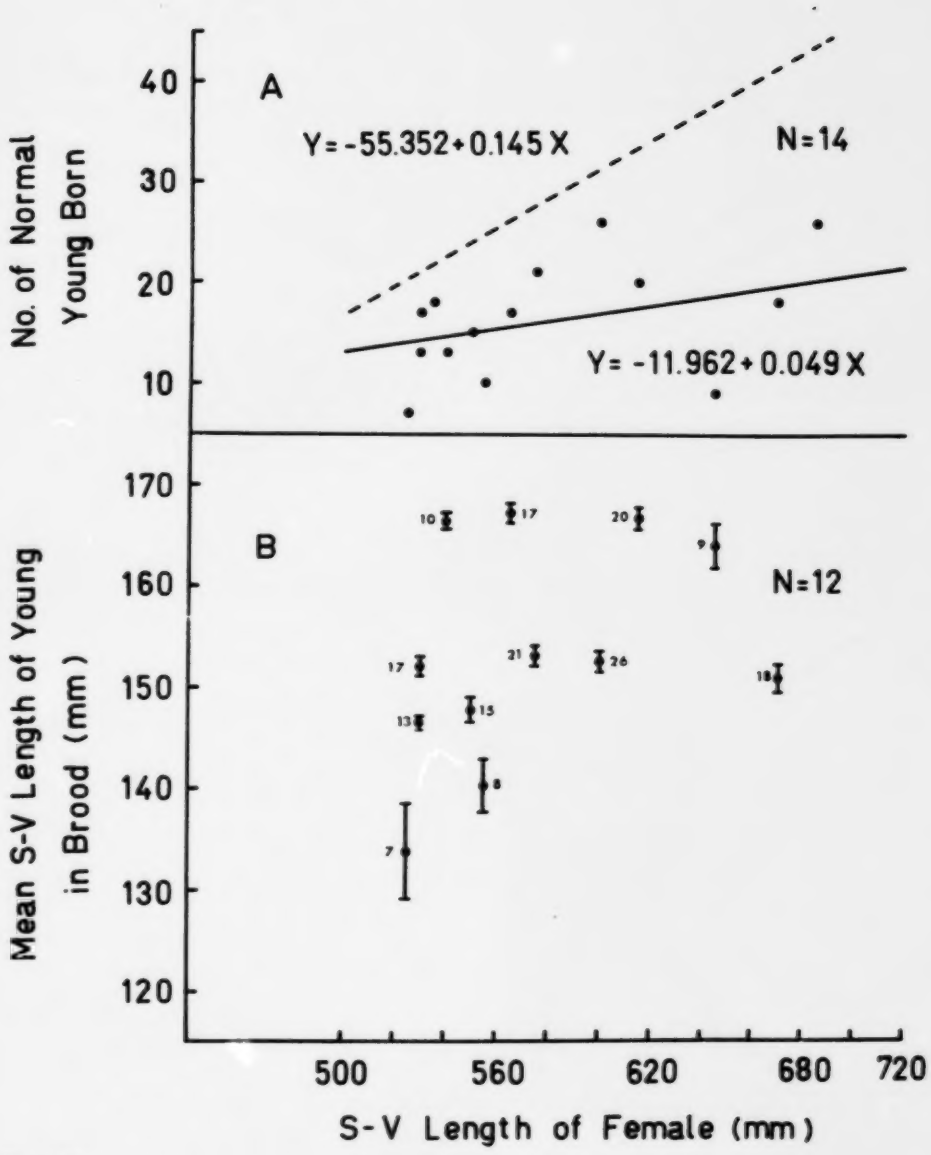

Figure 12
A. Regression of brood size on size of female for females from summer 1972 (solid line) and theoretical regression for denning females in spring 1972 (broken line). N = sample size.
B. Average size of young in brood vs. size of female. Vertical lines are ± 1 S.E. about mean. Numbers represent brood sizes. N = sample size.

were born dead; this number was quite variable, and some of these young were in poor condition. Several litters contained up to three deformed young, all dead. The mean number of normal young, both live and dead, of the 14 complete and separate broods was 16.43 (S.E. = 1.54), larger litters tending to come from larger females (Figure 12A). For comparative purposes, the dotted line in Figure 12A represents the theoretical regression of brood size on size of female for females in spring 1972. This line is an extrapolation of data for 1972 presented in Figure 8, based on the known loss of reproductive potential during gestation (Figure 11).

The sex ratio of the five litters born together was 57 males: 54 females (plus one unsexed). Table 3 summarizes the sex ratio determinations performed on the 14 intact broods using the method for estimation of proportions in cluster sampling (Cochran 1963: 64–67) . All normal-looking young were used in this analysis except for one unsexed animal.

Ninety-one males and 91 females from the 14 litters were measured. The average S–V length of the males was 154.88 mm (S.E. = 1.15) and that of the females 154.00 (S.E. = 1.03). A t-test on the means of the two groups revealed no significant difference between them. Larger young tended to come from larger females (Figure 12B), but the correlation was not high.

Reproductive Cycle

In all months, females were found in what appeared to be virtually all stages of the reproductive cycle, other than pregnancy. Even in June, apparently mature but unmated females were found away from dens. It was not known, however, how long ago these snakes had dispersed from their dens and how much growth had taken place in that time. Quantitative fat body measurements were not made, but potentially reproductive females generally had large amounts of fat covering the abdominal viscera ventrally, whereas immediately postpartum or immature females had little or no fat.

Mating of these snakes was most evident at dens in spring in the form of mating "balls" (Aleksiuk and Gregory 1974; Gregory 1971) and generally covered a period of four to six weeks. In late summer and fall of 1972, however, 27 females containing sperm in their oviducts were caught. In all but one (a postpartum female) the ovaries were in reproductive condition or nearly so. Fourteen snakes bore totally non-motile sperm, and about half of the sperm complement of another snake was non-motile. In all other cases, and in snakes in spring, the sperm all seemed to be completely motile. Two snakes caught in August of 1971 possessed copulatory plugs, as did one of the females containing sperm in August of 1972.

Fourteen postpartum females were examined: 13 in late summer and fall of 1972 and one in spring 1973. In general, there appeared to be a direct relationship between degree of reproductive development of the ovaries and the condition of the fat body. Three of the postpartum females were apparently able to reproduce again. Postpartum females accounted for 5 of the 6 non-reproductive females in the 501- to 650-mm interval shown in the totals column of Table 2.

Males

A total of 118 male snakes were examined in 1972. Total weight of testes per S–V length of animal was low in spring, rising to a level almost four times that of spring by mid-July (Figure 13). Thereafter, testis weight declined gradually until September, when it again reached the spring level. The abrupt rise in early summer shown in Figure 13 is due to the fact that most animals collected in spring came from a den in which emergence and subsequent dispersal were particularly late; the dispersed snakes found at this time probably came from earlier dens.

In each animal, presence or absence of sperm was noted for each testis, epididymis, and vas deferens. For each organ, the average number containing sperm per animal was calculated for each sample day (Figure 14). Most animals had no sperm in their testes during spring, but the average number of testes containing sperm per animal rose gradually through the second half of June and in July. Throughout August, most males had sperm in both testes. This was more or less coincident with the decline in the ratio of weight of testes to length of animal. By fall, most males had no sperm in either testis.

The epididymis was often difficult to locate precisely, and consequently, the findings that follow may not be completely reliable. Figure 14 indicates that sperm were most often found in the epididymis at the same time as they were found in the testis (that is, in August). The snakes tended to have sperm in their epididymes fairly frequently in spring and fall and less so in early summer.

Table 3
Sex ratios of 14 intact broods from summer 1972 and estimated proportion ($\hat{P}$) of males in total sample with estimated standard error (after Cochran 1963: 64–67)

Litter no.	No. normal young	No. males	No. females
i	X_i	Y_i	
1	26	15	11
2	20	11	9
3	25	9	16 (+ 1 unsexed)
4	17	6	11
5	18	6	12
6	9	3	6
7	7	5	2
8	13	7	6
9	10	6	4
10	21	9	12
11	18	9	9
12	17	8	9
13	13	5	8
14	15	8	7
	229	107	122

$$\hat{P} = \sum_{1}^{14} Y_i / \sum_{1}^{14} X_i = \frac{107}{229} = 0.467$$

$$S.E.(\hat{P}) = \sqrt{\frac{\{\Sigma Y_i^2 + \hat{P}^2 \Sigma X_i^2 - 2\hat{P}\Sigma Y_i X_i\}}{n(n-1)\,\bar{X}^2}}$$
$$= 0.028 \text{ (where } n = 14)$$

Almost all vasa deferentia examined in spring and fall contained sperm, but the number dropped during early summer, rising again when sperm also began to appear more frequently in the testes, in August.

Some of the males collected at this time of year contained non-motile sperm in their reproductive tracts, as did several females that had mated in late summer or fall of 1972.

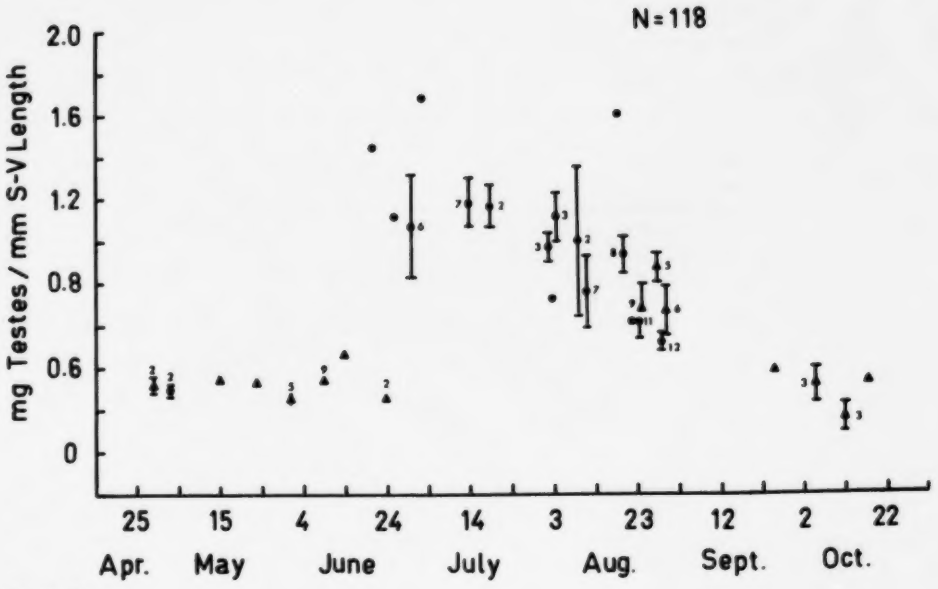

Figure 13
Weight of testes per S–V length of animal for males throughout the active season of 1972. All points are means for a particular sample day; vertical lines are ± 1 S.E. about mean. Numbers indicate sample sizes greater than one. Triangles = snakes caught at dens; dots = snakes caught elsewhere; N = sample size.

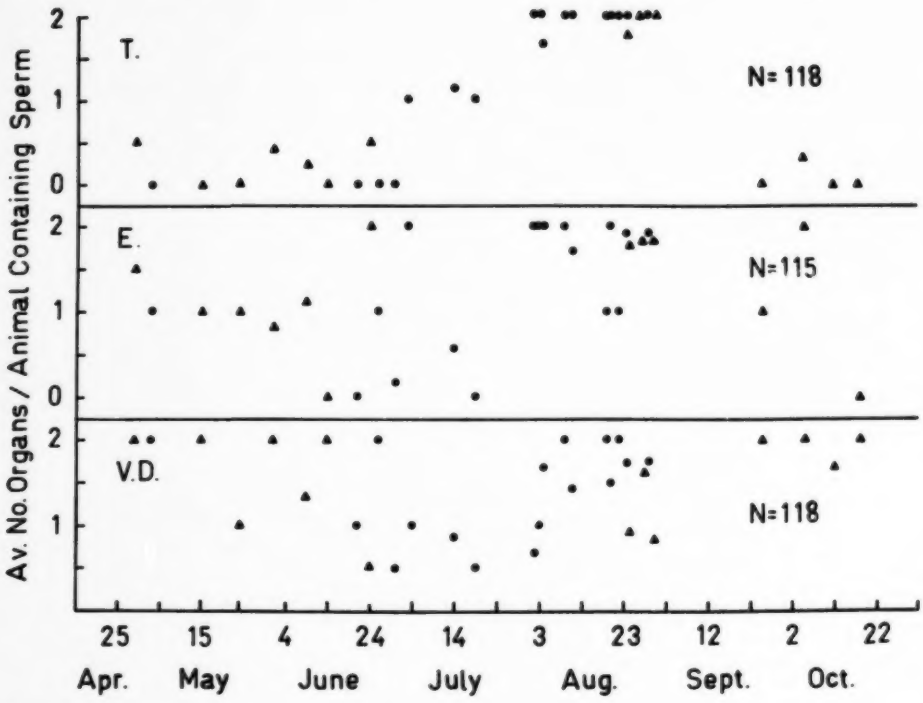

Figure 14
Average number of testes (T.), epididymes (E.), and vasa deferentia (V.D.) containing sperm per male per sample day in summer 1972. Triangles = snakes caught at dens; dots = snakes caught elsewhere; N = sample size. See Figure 13 for daily sample sizes.

Discussion

Growth

Previous growth studies of *T. sirtalis* (Carpenter 1952*a*; Fitch 1965; Platt, personal communication) have shown that females grow faster than males and that great individual variation exists in growth rates. In both sexes, the rate of growth decreases with age. My data agree with this and indicate that females are more variable than males (Figure 4).

It is difficult to compare the growth of adult *T. sirtalis* from the Interlake of Manitoba with that of adults from other parts of the distribution range of this snake because of the scarcity of formal growth analyses in the literature. Fitch (1965) described the growth of the species in Kansas, based to a large extent on relatively short-term recaptures. His description of populations inhabiting the University of Kansas Natural History Reservation seems to suggest annual growth rates similar to those shown by adult snakes in my study. Carpenter's (1952*a*) scatter-plot data for *T. sirtalis* in Michigan also agree with my results in terms of annual growth, but his growth curves do not seem to agree with his scatter-plot data, and they indicate a much slower rate of growth. The reasons for this apparent conflict in Carpenter's paper are not clear. Platt (personal communication) calculated annual growth rates for *T. sirtalis* in Kansas that are higher than any reported elsewhere.

Growth in *T. sirtalis* appears to be subject to much variation. In this study, growth rates of the males, and presumably of the females, were somewhat different in every year. The reasons for these different growth rates are not obvious. Both Fitch (1965) and Platt (personal communication) found that growth rates were greater in years with higher rainfall, presumably because of the beneficial effects on the amphibian populations preyed upon by the snakes. In the Interlake region, rainfall did not differ notably among the years of the study.

Fitch (1965) also found a two-fold difference in growth rates between individuals in two populations of *T. sirtalis* in separate localities in Kansas. This difference appeared to be related to food supply. Obviously, the potential for a great deal of variation exists, and it is possible that *T. sirtalis* in Manitoba may be able to grow as much in the three months available for major growth as do individuals in, for example, Michigan, in five months (Carpenter 1952*a*). Attempts to compare growth rates of this species in widely separated geographical localities are probably futile, unless detailed information on the factors affecting growth in the different areas becomes available.

Growth rates of subadult snakes in the populations under study are also difficult to assess because little is known about this stage of the life cycle. It is not even known how long an active feeding season they have available for growth, although it may be longer than that of the adults (Gregory and Stewart 1975). Most information on growth of the young is indirect. Measurements of red-sided garter snakes collected by Cook (personal communication) in the spring of 1961 in Saskatchewan, where the climate is similar to that in my study area, revealed that the smallest animals were between 200 and 270 mm S–V length. No animals were present in the 270- to 330-mm interval, and the remainder of Cook's size-frequency distributions were similar to those which I obtained. The smallest snakes he found were undoubtedly first-year animals and, unless an age-group is missing, the next smallest represented the second-year class. On this basis, I suggest that the size of the group of smallest males seen at the Interlake dens also represents second-year snakes. In the case of females, however, the size class of smallest animals is less clearly defined, and it is possible that this group consists of both second- and third-year individuals. This is particularly likely when the rather large mean size of the group and the extreme brevity of the growing season are considered. Corroborating evidence comes from scatter-plots (not shown) of lengths of snakes captured throughout the year in the Interlake. Although no clear separation of age classes is evident in these plots, it would seem that after their first complete summer of life, young males are able to reach body lengths of 450 to 500 mm, and females of 500 to 550 mm. These approximate figures are consistent with the conclusion that the youngest male snakes in denning populations are in their second year and that at least some of the smallest females are also second-year animals.

The sizes of second-year males found in this study are similar to those described by Carpenter (1952*a*) and Fitch (1965), but lower than those studied by Platt (personal communication). Since the second-year class could not be precisely defined for females, comparison with other studies is difficult. In view of the above discussion, however, it seems pos-

sible that second-year females in the Interlake are smaller than those reported elsewhere.

Population Characteristics

Structure and Numbers

Several authors have expressed reservations about the usefulness of mark–recapture estimates (Manly 1971; Eisenberg 1972; Roff 1973*a*, 1973*b*). On the basis of the sample sizes obtained and the degree of accuracy attained by Carothers (1973) using the Jolly index, however, it would seem that the results of this study are realistic and are certainly indicators of at least relative population sizes. The good agreement obtained between the Jolly and the Petersen estimates is not surprising, since the former is simply an extension of the latter, and high correlation of the two is to be expected. In any case, single-species aggregations of denning snakes of the large sizes cited here have not been reported elsewhere.

Little is known about size structures of denning populations of *T. sirtalis*. The size-frequency distributions shown by Fitch (1965) are similar to mine (Figures 6 and 7), at least for the males. The degree of overlap of size groups is so great that it is impossible for me to determine how many age-groups of each sex exist. Presumably at least four are present, since individuals of both sexes have been found at dens three years after original marking. Fitch felt that females in Kansas may sometimes live for seven years or more.

In contrast to the Interlake situation, large dens in Riding Mountain National Park in Manitoba apparently contain juvenile snakes as well as adults. Smaller dens of *T. sirtalis* near Toronto, Ontario, also include the young (Weller, personal communication). Cook (personal communication) found juveniles near a hibernaculum used by adults at Estevan, Saskatchewan. In studies of other species of snakes, Volsøe (1944) and Prestt (1971) found young *Vipera berus* hibernating with adults, but Parker and Brown (1973) felt that young of three species in Utah generally denned elsewhere in their first few years. Other authors do not consider this question specifically.

The autumn sex ratios of the adult populations in this study, assuming that all adults den at the large communal hibernacula, are close to 1:1. This is presumably the case in spring as well. Only in the fall of 1969 was there any evidence of an uneven sex ratio; in that year there was a slight surplus of males. On the basis of population estimates (Table 1), it would appear that there was a large surplus of males every year. The magnitudes of error in the estimates for each sex are sufficiently different, however, that they cannot be compared fairly in this way.

Information on sex ratios in the literature is conflicting. Platt (personal communication) found a surplus of male *T. sirtalis* in his study, whereas Fitch (1965) found the opposite to be the case. Carpenter's (1952*b*) population estimates also indicate that females may be more numerous than males. The approximately 1:1 sex ratio at birth obtained for the snakes in my study is in general agreement with Carpenter (1952*b*), Martof (1954), and Fitch (1965), although all found a slight surplus of males. Platt (personal communication), however, found that the sex ratio at birth of the *T. sirtalis* populations he studied was heavily biased in favour of males. The reasons for these variations are not apparent; possibly they are caused by differences in sampling methods.

On the basis of my data on sex ratios, there is little evidence of any difference in survivorship between the two sexes. It might be expected that older females would be more susceptible to predation or to the effects of severe weather conditions (or both) than other members of the population since, when gravid, they bask more than other snakes. This would explain the higher male to female ratio at the den in the fall of 1969, since the summer of that year was particularly cold. The reversion to a nearly 1:1 sex ratio the following autumn, assuming that an even sex ratio is the norm, can be explained solely on the basis of age distribution. Older age-groups comprise a very small proportion of the total population in any year (Figure 6 and 7). Consequently, it is probable that an unusually high rate of loss of any group of adult snakes in one year would not be detectable in the following year because most of those snakes would probably not have survived anyway.

Population Dynamics

A common characteristic of animals living in areas of variable or unpredictable climate is variability in population size (Pianka 1970). The Interlake populations of *T. sirtalis* appear to be no exception. Although good estimates of population sizes with relatively low variances were obtained only for males, it seems that the Den One population dropped drasti-

cally from a high of about 8,000 snakes in 1969–70 to about half that size the following year, and that this lower level was maintained in 1971–72. A swing upward again is indicated for 1972–73, but these estimates are not very accurate.

The survivorship figures obtained from the Jolly analysis represent, strictly speaking, the probability of survival *in the study area*. In this instance, however, these figures are taken as indicating survival in general, since individual snakes appear to use the same den from year to year. These figures (Table 1) are interesting for two reasons. First, overwinter survivorship is relatively low, indicating a significant loss of animals during hibernation. Hawley (personal communication) found large numbers of dead snakes below ground, in a den at which he was working at Narcisse, Manitoba, in the spring of 1973. Apparently, many of these had been frozen, but most had their heads chewed off as though they had been attacked by small mammals. Snowfall was light in the winter of 1972–73; this lack of insulation might have accounted for the snakes freezing underground. Hirth (1966) found similar rates of overwinter mortality for three species of snakes in Utah, and Carpenter (1952*b*) felt that the young of three species of garter snakes in Michigan may have experienced high winter mortality. Carpenter in fact recorded one definite instance of winter kill in *T. sirtalis*.

The second important point concerning the survivorship figures is that they are similar for summer and winter among all years. This suggests that the population decline between 1969–70 and 1970–71 was not due to decreased survivorship of adults per se but to other causes.

The size-frequency data for males (Figure 6) support this idea. Except for fall 1970 and spring 1971, the second-year snakes were the dominant age-group; the den population declined during the 1970–71 overwintering season. This is less clear in the data for females (Figure 7) because of the small sizes of the samples and the difficulty in distinguishing age-groups. In autumn 1970 and spring 1971, the second-year males comprised a small part of the population, suggesting that the population decline might have been caused by a reproductive failure in 1969, when these animals would have been born. Subsequent low survival of the young of that year might also account for the decline. The same argument presumably applies to females.

Weather, through its effects on populations of prey animals, can greatly influence the amount of food that snakes obtain, and consequently the amount of energy that they have available for reproduction the following year (Platt, personal communication; Parker and Brown 1973). Winnipeg weather records for 1968 indicate no abnormal amounts of rainfall or sunshine nor exceptional temperature deviations. In 1969, however, June was exceptionally cold: maximum, minimum, and mean temperatures were all below normal, and on two days, June 13 and 20, frost was recorded. In addition, July was cooler than usual. Rainfall was high in both months, resulting in further cooling effects. These weather conditions probably had a profound influence on reproduction that year. By June, the snakes presumably had left their hibernacula (Gregory 1971), ovulation should have occurred (Figure 10), and gravid females should have been incubating their broods. Since gravid females spend much time basking in exposed areas, the late June frosts may have caused the deaths of a number of gravid females, and hence of unborn young. The sex-ratio data discussed above are consistent with this possibility.

More important, however, is that embryonic development of young was probably affected. Fitch (1960) found that gestation periods of *Agkistrodon contortrix* were extended in summers characterized by low temperatures and high cloud cover. Blanchard and Blanchard (1940), Fox (1948), and Zehr (1962) have shown that embryonic development in *T. sirtalis* is retarded by low temperatures. This can be critical when the summer is short. Fox's work further suggests that development may be arrested completely under very cool conditions.

The cool summer of 1969 may also explain the failure of the Den One population to increase again in 1971–72. The second-year snakes recruited into the population in that overwintering season were produced by the breeding of the 1969–70 population. Since the 1969–70 population was large, and the summer of 1970 was not particularly cold, reproduction should have been fairly successful in 1970, resulting in a population increase in the fall of 1971. The cool conditions existing in the early summer of 1969, however, might have inhibited feeding of the snakes so much that the energy requirements for reproduction the following year were not completely fulfilled.

Platt (personal communication) feels that large changes in population sizes of snakes, including *T. sirtalis*, in Kansas may be due mainly to changes in fecundity or survival of young. This is probably also true in the Interlake. Parker and Brown (1973) arrived at similar conclusions for *Coluber* in Utah. They felt that fecundity and survivorship are influenced by changes in population levels of prey species; Platt in fact monitored the prey populations in addition to the snake populations. The underlying implication of these studies is that weather is actually the ultimate factor in limiting snake populations because it can reduce the prey species, thus limiting the food supply of the snakes. In the Interlake, weather may act as a more proximate limiting factor by directly affecting fecundity, and hence snake-population levels.

A dramatic demonstration of the effect of weather on populations of *T. sirtalis* in the Interlake has occurred since this study was completed. The Den One population was completely exterminated in 1973–74, presumably because of extensive flooding caused by spring melting of the unusually large snowfall of that winter (Stewart, personal communication). Other dens were apparently affected to varying degrees. Such large-scale extinctions are probably fairly rare.

In addition to weather, predation must also be considered as a significant source of mortality. Carpenter (1952*b*) and Fitch (1965) have documented the important predators on *T. sirtalis* in their study areas. In the Interlake, known predators on this species are crows (Gregory 1971), owls (Weselowski, personal communication), coyotes (Pastuk, personal communication), and skunks (Penny, personal communication). Automobiles also play a major role in annual mortality. On the basis of available literature and personal communications, I find it probable that *T. sirtalis* is not a preferred food of any single predator, but an occasional food of many. Humans, however, may be major predators, since garter snakes in the Interlake are collected in large numbers for commercial purposes.

Reproduction

Potential Fecundity

In most reptiles, reproductive potential varies directly with the size of the female (Tinkle 1962). My data suggest that this is true for *T. sirtalis* in the Interlake. Fitch (1965) found similar results for the same species in Kansas, but the correlation does not appear to be as high. Whereas my data show a linear increase in fecundity with increasing body size, Fitch found a levelling off at an age of about four years and perhaps even a decline in very old snakes. It also seems that the reproductive potential is higher at any given body size for Interlake than for Kansas *T. sirtalis*. Fitch's data were obtained by palpating gravid females in summer, and mine by dissecting unovulated females in spring. Also, my samples might not have included individuals as old as Fitch's oldest females. My samples did, however, include the sizes at which he detected the levelling-off effect. Tinkle, Wilbur, and Tilley (1970) described a similar situation in the lizard *Uta stansburiana*, in which the correlation between the clutch size and body size was higher in northern than in southern populations.

Carpenter (1952*b*) and Fitch (1965) found that not all adult female *T. sirtalis* were gravid in any given year. Fitch showed that there was a positive correlation between age-group and the proportion of gravid females in that age-group. These data, however, were compiled from snakes captured in the summer. Platt (personal communication) believed that most adult females in the populations he studied were gravid in summer, although a smaller proportion might have reproduced in years when food was scarce. In general, both Platt and Fitch found that the youngest reproductive females were second-year snakes, although Platt found that first-year females reproduced in years when food was abundant. In the Interlake, all males are probably capable of reproduction in their second year, but some females probably do not breed until their third year. My data (Table 2) from denning populations and dispersing snakes suggest that females less than 400 mm S–V length in spring are not capable of reproduction, and that the percentage of reproductive females increases steadily with size. Above 500 mm, virtually all females are potentially reproductive. Five of the six females in this size category that were not reproductive had obviously borne young the previous year.

Carpenter (1952*b*) felt that most of the nongravid adult females he caught had simply not mated. My work (Figure 9) indicates that this may be the case for the smallest potentially reproductive females. In fact, Hawley and

Aleksiuk (1976) indicate that the probability of courtship and mating increases with increasing body size of the female in Interlake *T. sirtalis*. If so, the non-reproductive females, which are almost always small, and the smallest potentially reproductive females may go unmated. The status of the unmated but mature females caught away from dens in the early summer of 1972 is not clear. Possibly these snakes were early dispersers and, though immature at the time of dispersal, had developed to an apparently reproductive condition by the time I caught them.

The reason for the difference in reproductive potential between 1972 and 1973 is unknown. It is possibly related to differences in food supply or weather conditions that I am not aware of.

Development of Young

Yolk deposition in mature eggs of *T. sirtalis* in the Interlake apparently occurs following emergence from hibernation and prior to ovulation. This agrees with Bragdon's (1952) finding that mature ovocytes increase rapidly in volume in spring, before they ovulate. Platt (personal communication) feels that the abdominal fat body is probably not an important source of nutrients in this development.

Ovulation may occur any time from mid-May on. Time of ovulation undoubtedly has great bearing on time of birth, since gestation presumably begins with ovulation. It has been observed previously (Cieslak 1945; Betz 1963*a*, 1963*b*) that ovulated eggs may enter the oviduct on the opposite side of the body. The frequent discrepancy between the number of eggs *in utero* and the number of ovulation scars in the ovaries, however, is not referred to in the literature. Betz (1963*a*, 1963*b*) found that yolk masses sometimes undergo resorption *in utero* in *Natrix*. Although this might have accounted for some of the differences observed, it is also possible that some eggs might simply have failed to reach the oviduct upon ovulation. Other sources of loss during embryonic development are well-known: ovulated eggs may fail to be fertilized (Fitch 1965) or otherwise fail to develop (Cieslak 1945); embryos may develop abnormally and die (Martof 1954; Betz 1963*b*) or be aborted (Fitch 1965); apparently normal young may be stillborn (Fitch 1965); or dead young may be retained in the body following parturition (Betz 1963*a*). Observations similar to the above were made in this study, but it was my impression that loss of eggs upon ovulation, abnormal development, and stillbirths were most important. The significance of this rather high rate of loss is not known.

Birth in Interlake *T. sirtalis* may occur any time from the end of July until the end of September. As previously noted, most births were observed in captive females. The later births reported here may be unnatural, since many authors have expressed the opinion that captive female snakes may show a retarded gestation. It seems likely, however, that some female snakes may give birth later in the year because of the variation in timing of activities at different dens. Times of emergence from dens and dispersal to summer habitat may vary by as much as a month in my study area. Some dens are not empty until mid- to late June in some years, and females from such hibernacula presumably give birth much later than do others. Date of birth probably depends on several factors, such as date of spring emergence and dispersal, date of ovulation, and weather (especially air temperature and incoming radiant energy).

The disintegration of the ovulation scars by the time of birth, as noted in this study, is in contrast to the findings of Cieslak (1945) and Bragdon (1952). These authors felt that these scars did not regress markedly until after gestation was terminated.

The average litter size obtained in this study is similar to the findings of Carpenter (1952*b*), Zehr (1962), Fitch (1965), and Platt (personal communication). Average number of live young was not calculated because it was not known to what extent the captive conditions were responsible for stillbirths. A comparison of the regression of brood size on female body size with the regression predicting litter sizes for spring females (Figure 12A) indicates that the method used for calculating potential fecundity tended to overestimate. That is, the amount of annual growth predicted from this figure for females bearing specific numbers of young is much greater than that actually obtained from the formal growth analysis. The variance about the upper line in Figure 12A has not been calculated, but it is undoubtedly very great. Average size of the newborn young recorded in this study is somewhat smaller than the figures obtained by Carpenter (1952*b*), Fitch (1965), and Platt (personal communication), but larger than those reported by Martof (1954).

Reproductive Cycles

Biennial reproductive cycles in females have been reported for several species of snakes. Tinkle (1962) has reviewed the literature on reproductive cycles for viperids, as has Prestt (1971) more recently for *Vipera berus*. Saint Girons (1957) concluded that, in *Vipera aspis*, longer reproductive cycles occur in colder climates because of the short amount of time available for accumulating energy reserves.

Biennial reproductive cycles have not been reported for *T. sirtalis*, but they might be expected in the Interlake populations. Although some potentially reproductive females may go unmated each year, most denning females above 500 mm S–V length are able to reproduce. This is in contrast to the findings of Rahn (1942), Tinkle (1962), and Prestt (1971). On the basis of presence or absence of ovulation scars, size of ovarian follicles, and size of fat body, these authors found that denning populations of their respective species could be separated into two classes of adult females: reproductive and non-reproductive. The ratio was not 1:1 in each case, but it was clear that a biennial cycle was involved in each. Prestt (1971) obtained other evidence, including yearly records of individual females.

In this study, obviously postpartum females were occasionally found at dens. A majority (62.5%) were definitely not able to reproduce, as evidenced by the condition of the fat body and the sizes of eggs in the ovaries; but the remainder were. Whether or not females are capable of breeding in successive years may depend on how early in the summer they bear young as well as on the availability of food after they give birth. Both of these, in turn, probably depend on weather. The small number of obviously postpartum females found at dens may indicate that either most females reproduce every year and are no longer recognized as postpartum by the time they appear at the dens or that they do not return to the dens after giving birth. If the latter is the case, females that give birth late in summer may feed for so long that they simply do not have time to return. Perhaps as a result of this they die from exposure in the autumn or they find other hibernating sites, such as those which might be used by the young-of-year.

The male reproductive cycle is an annual one. This is not surprising, since males do not have to invest as much energy in reproduction as females do. Maximum testis development occurs in midsummer, coinciding with the appearance of mature sperm (Figure 13). Sperm appear to move rapidly from the testes and are present in the vas deferens throughout most of the year. Males are obviously able to reproduce before they hibernate in the fall. These results are compatible with those of Cieslak (1945) and Fox (1952, 1954). They also account for the occurrence of late-summer and autumn mating in these snakes, although the significance of such mating is not clear (Aleksiuk and Gregory 1974).

The reason for the occurrence of non-motile sperm in the reproductive tracts of males and in mated females in the fall of 1972 is also not clear. No reference is made to this phenomenon in the literature, and it is possible that these sperm could have been dead. On the other hand, such sperm might overwinter in this condition and become active the following spring. Why some snakes should have living, motile sperm and others living, non-motile sperm is not known.

Life-History Strategy

Throughout its range, populations of *T. sirtalis* appear to fluctuate considerably in size. Such fluctuations seem to occur in response to variations in weather, either directly or indirectly. In the Interlake of Manitoba, where the climate is extreme and highly variable, population fluctuations of *T. sirtalis* are particularly great, and drastic declines in population size have been observed. Despite this, the species is generally abundant in the Interlake, even during population lows, and is the most frequently encountered of the four species of snakes occurring there. Population declines are possibly minimized because they mainly involve reduced reproduction or poor survivorship of young (or both) rather than increased adult mortality. Presumably, adult survivorship can be attributed to physiological adaptation to the extreme environment (Aleksiuk 1970; Vincent 1971; Hoskins and Aleksiuk 1973*a*, 1973*b*). More serious population declines involving high adult mortality do, however, occur occasionally.

In highly variable environments, populations must be able to increase rapidly after a decline or else run a high risk of extinction; selection in such situations should favour individuals with "r" characteristics (Pianka 1970). Population increase was not observed in this study, but denning populations of *T. sirtalis* have been well known in the Interlake for a long time. Presumably, fluctuations in

both directions are a normal feature of their life history. Because of differences in environmental stability and severity, and the resultant population effects, Interlake populations of *T. sirtalis* might be expected to have a higher intrinsic rate of natural increase, r_{max}, than do populations farther south.

As Cole (1954) has pointed out, an important contribution to the achievement of a high r_{max} is made when first reproduction occurs at an early age. In the Interlake region, male *T. sirtalis* are apparently capable of reproduction by the second year of life, in accordance with the findings of other authors (Carpenter 1952*a*; Fitch 1965; Platt, personal communication). In terms of contribution to future population increase, however, the age at which females first reproduce is more significant. In the Interlake, it appears that some females may reproduce in their second year, but many do not until their third year. This is in contrast to findings for more southerly populations, in which first reproduction usually takes place in the second year (Carpenter 1952*a*; Fitch 1965; Platt, personal communication) and sometimes even in the first year (Platt, personal communication).

Age of first reproduction in Interlake females is probably the result of a balance between two factors, the evolutionary advantage of early reproduction and a physiological limit on the annual amount of growth possible for the individual. This limit to growth is imposed by the extreme shortness of the growing season. Adult garter snakes in this area appear to spend only about three months of every year actively feeding and growing (Gregory and Stewart 1975). By comparison, Michigan has a five-month growing season (Carpenter 1952*a*). Platt (personal communication) also indicates a longer active season for his populations in Kansas.

Growth of adult females, however, is less important to population increase than growth of immature individuals, since adults that have already reproduced once have made their major contribution to population increase. Even if first reproduction does not occur until the third year of life, the increase in size of Interlake females in their first year is obviously great. First-year males also exhibit considerable growth. How this large amount of growth is accomplished is puzzling, especially when one considers that some births may occur very late in summer. The most likely explanation is that immature snakes extend their growing period by feeding late in their first autumn and early in their first spring (Gregory and Stewart 1975). Little is known about this stage of life, since recently born snakes are rarely found.

Increased brood size can also be important in raising the r_{max} of a population. Results of this study indicate little difference between average litter sizes of females from the Interlake and from elsewhere. Potential fecundity, however, may be higher in snakes from the Interlake, particularly in larger females, as is suggested by comparison with Fitch's (1965) data for Kansas snakes. Since many of the gravid females examined in this study had more ovulation scars in their ovaries than ova in their oviducts, it is clear that the difference between potential and realized fecundity is not simply an artifact of the method used to estimate reproductive potential. Perhaps in some years the litter sizes observed here are exceeded; it is also possible that a high rate of loss of eggs is normal in the Interlake area.

With respect to age of maturity and litter size, there are evidently few real differences between *T. sirtalis* from the Interlake and *T. sirtalis* from elsewhere. Other aspects of life history, however, may be important in influencing rates of population increase. For example, the relatively high potential fecundity shown for Interlake females means nothing unless a large proportion of the mature females in the population mate and produce young; this is especially important when one considers the severely limiting nature of the Interlake climate. On the other hand, because of the short summer available to these animals, it is obvious that individuals cannot afford to spend much time each year searching for mates. In an earlier paper (Gregory 1974), I suggested that rapid breeding in the Interlake snakes is probably facilitated by the combination of communal denning with the particular way in which these animals emerge from hibernation in spring. Males emerge in large numbers early in spring, whereas females emerge in smaller numbers throughout the spring season. Immediately upon emergence, these females are sexually attacked by large numbers of males and are fertilized by probably one male. The females then disperse to their summer habitat shortly thereafter. It is likely that a high proportion of females in these populations are mated as a result of this pattern of sexual activity (Figure 9). Males remain at the den site for some time, presumably mating more than once. Gibson and Falls (1975) regard such mating behaviour as the

result of intra-sexual selection among males for access to females, but other interpretations are possible. One important advantage of communal denning may be that large numbers of mature animals are congregated in one place during the breeding period, thereby allowing this mating system to operate. Data collected in this study (Figure 9) indicate that most mature females do mate. The unmated, but apparently mature, females caught in summer may have been immature at the time of spring emergence from hibernation. Complex emergence and mating systems such as described in Gregory (1974) have not been previously reported. In more southerly areas, where time is not at such a premium each year, they may be less likely to evolve.

This pattern of spring activity may be advantageous in other ways. For example, the actual producers in the population, the mature females, spend a minimum of time in an active, non-feeding state at the den and more time incubating their broods. Although gravid females feed significantly only in early summer (Gregory and Stewart 1975), the time available to them for growth and other activities may well be more than three months, at least for those that emerge early in spring. The bulk of the population that remains at the den for any length of time in spring is male and therefore somewhat more expendable. The staggering of emergence times of the female population, despite the apparent advantage of early dispersal, may also result in at least partial reproductive success in the event of a severe cold snap early in spring. If all the females dispersed early, such a cold period could eliminate reproduction entirely in that year, but the reserve of female snakes that emerge later may partially compensate for such a loss.

Evidently, it is advantageous for all the adult members of the species to overwinter in large communal groups. At first glance, however, communal denning appears to represent a great cost to the individual. For example, *T. sirtalis* from dens in the Inwood area regularly move from about 4 km to as much as 18 km when dispersing from dens to their summer habitat, which consists of large marsh belts (Gregory and Stewart 1975). Such long-distance movements have not been recorded for snakes before and presumably require considerable expenditure of energy. There are no obvious sites suitable for use as hibernacula by large numbers of snakes in or near the summer habitat, although small groups or individuals could possibly be accommodated in potential hibernacula, such as abandoned ant mounds. On the other hand, these long-distance migrations may explain why juvenile snakes are not found at the communal hibernacula. For the young-of-year, there is no obvious advantage in hibernating in large numbers, and they expend less energy if they remain in the summer habitat where they were born, for at least their first winter. Because they are small, they can use many small overwintering sites that the adults would physically be unable to use. In fact, it may be so difficult for the adults to find hibernacula near the summer habitat that they are simply forced to move as far as they do. If so, communal denning and its apparent benefits might have developed as a result of the movement pattern rather than vice versa. In any case, there is a developmental change in behaviour of the Interlake snakes between the juvenile and adult stages. Communal dens of *T. sirtalis* in other parts of Manitoba include young-of-year; possibly, summer dispersal occurs over much shorter distances in these places.

T. sirtalis appears to be very sensitive to fluctuations in weather and resembles an "r-selected" species (Pianka 1970) throughout its range. In the Interlake of Manitoba, where the climate is particularly severe and unpredictable, and the growing season short, population levels are highly variable, but Interlake snakes do not breed earlier nor do they have larger litter sizes than snakes found farther south. Their annual cycle, however, includes such characteristic features as communal denning, complex spring emergence and mating behaviour, and long-distance dispersal, the latter two being unusual in snakes. Although the cause–effect relationships of these features have not been determined, they may be closely linked to the problem of maximizing reproduction in the face of severe environmental adversity.

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